

A fuzzy classification of moorland ground beetle (Coleoptera: Carabidae) and plant communities

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Summary. Ground beetles and vegetation were sampled at 74 sites on an area of moorland in Northumberland. Pitfall traps and permanent quadrat points were used to obtain ground beetle presence/absence and vegetation percentage cover data sets. Each data set was ordinated by Detrended Correspondence Analysis (DECORANA) and classified by fuzzy clustering. Five ground beetle communities and three broad vegetation types were recognised from the analyses of each of the data sets. Spearman rank correlation indicated that the distributions of the sites in both ordinations were primarily related to soil environmental variable measurements – pH, moisture content, dry bulk density and organic matter content. The groupings of sites obtained from the carabid and vegetation analyses were compared using the log-likelihood ratio test in a contingency table and by Procrustes rotation of the vegetation ordination scores onto the ground beetle ordination scores. Results obtained indicated that there were variations in the closeness of the associations between the ground beetle and vegetation groups recognised. The potential for using the techniques to allow predictions of ecological change to be made are discussed.

Key words: Carabid communities – moorland plants – DECORANA – fuzzy clustering – environmental variables

Introduction

Economic pressures over the last four decades have increased livestock numbers in hill areas (Eadie 1984). The increased grazing pressure has resulted in significant changes in the natural vegetation of these areas. Of particular significance is the general regression in plant communities with a high conservation value such as those dominated by heather, with a concomitant increase in less valuable grasses and mosses (Ball et al. 1982). With increased awareness of conservation issues there is a need to find out how hill pastures can be managed to favour high conservation value plant and animal communities whilst at the same time maintaining viable agricultural activity on them (Eadie 1984). Small scale plot experiments have demonstrated the effects of changes in management practices on some vegetation types, e.g. reduced stocking density encourages the regeneration of heather, but extrapolation from the small plot to the large scale practical system operating in a true applied context is an extremely complex process (Grant & Maxwell 1988).

The research presented here forms part of a long-term project being conducted at the Ministry of Agriculture Experimental Husbandry Farm at Redesdale, Northumberland.

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This project is considering the practical situation at the farm scale and undertaking research aimed at creating and preserving a balanced interface between conservation and farming. The aim of the project is to study the interaction between grazing management, the stocking rate and output of sheep and the ecological quality of hill and upland grazing. The project is mainly concerned with the regeneration of heather and the effect of the application of sheep-grazing regimes of varying intensity on this regeneration and on the plant and animal communities of hill grazing.

Ground beetles have been shown to form a conveniently sized group for assessing changes in land use and/or management practices (e.g. Rushton et al. 1989; Rushton et al. 1990) and for quantifying conservation criteria (Eyre & Rushton 1989). In addition, more is known about the ecological requirements of individual species (Thiele 1977) than for most other groups of invertebrates except spiders (Rushton et al. 1987). Gardner (1991) recently studied the ground beetles on *Calluna*-dominated heath and recognised different communities dependent on soil wetness and *Calluna* development at each site. The aim of the research presented here was to obtain baseline data on the ground beetles on the study site prior to any heather regeneration and to investigate the factors influencing their distribution. The associations between ground beetle and vegetation communities were also examined. It was intended that the results would indicate whether such baseline information would allow predictions of invertebrate changes for any associated changes in vegetation cover to be made.

Materials and methods

Establishment of the project

The sample sites were on Ashtrees Heft, an area (117.16 ha) of sheep-grazed upland moorland at the MAFF Redesdale Experimental Husbandry Farm, Northumberland (O. S. Grid reference NY 8396). At the start of the project 100.5 ha of the heft was semi-natural rough grazing, lying to the south of a small semi-improved area of 16.66 ha. The heft faces north-east and is gently sloping, rising from 230–240 m at the northern boundary of the semi-improved ground to a maximum of 350 m at the south-western extremity of the heft, a distance of approximately 1750 m. Soil type is not uniform across the heft, with areas of more fertile mineral soils intermixed with peat above stagnohumic gley. Drainage is impeded, sometimes severely where slopes are minimal or absent.

A grid with grid square intersections every 75 mm was laid out on Ashtrees heft in June 1989 and the vegetation cover at fixed 1 m × 1 m quadrats positioned at 166 intersections was determined over a one month period from the second week of June. The cover data were classified using Two-Way Indicator Species Analysis (TWINSPAN; Hill 1979a) and seven vegetation types recognised. The species-by-site data matrix was also ordinated using Detrended Correspondence Analysis (DECORANA; Hill 1979b) in order to identify the dominant trends in variation in the vegetation across the site.

The heft was then divided into 2 areas of unequal size but with equivalent proportions of the different vegetation types in September 1989. The dividing fence effectively partitioned the 166 quadrats into two, one area (61.76 ha) with 73 quadrats and the other (54.4 ha) with 93. Following division the largest block of the heft (LSR) was subjected to a reduction in grazing pressure of 30% from 2.1 to 1.48 ewes/ha, whilst the smaller side (HSR) was maintained at the same high stocking rate. In addition, a detailed description of the soil environment present at each quadrat was made in January 1990. Soil samples were taken and pH, moisture content, organic matter content and bulk density determined following the methods described in Rushton et al. (1989).

Data collection

Ground beetle communities were sampled at 74 of the 166 permanent vegetation quadrat points on Ashtrees during 1990 – 32 on LSR and 42 on HSR. This was achieved at each site using five pitfall traps consisting of polypropylene pots of 7.5 cm diameter and 10 cm depth part filled with ethylene glycol-'blue' antifreeze. Traps were placed 1 m apart in a line through similar vegetation to that in

the quadrat. Traps were left for about 1 month and then emptied and refilled with fresh ethylene glycol solution. The contents of all 5 traps were pooled each month and stored in 70% alcohol prior to sorting and identification. Each site was sampled between May and September. The vegetation present in each of the 74 quadrat points was determined over a one month period from the second week of June 1990. A 1 m × 1 m quadrat containing 100 10 cm × 10 cm squares was used. All the plants present within each quadrat were identified to species and an estimate was made of their percentage cover values. A data matrix was created listing the presence/absence of the Carabidae species caught at the 74 sample sites. In addition, a data matrix was created containing the percentage cover of vegetation at each of the 74 sites in 1990. These data matrices were then subjected to multivariate analyses. The total number of ground beetles caught at each site and the vegetation percentage cover data were used in the calculation of diversity indices.

Multivariate analyses

Multivariate techniques were employed to allow objective analyses of the data to be made. Gauch (1982) concluded that two complementary multivariate analysis techniques, Two-Way Indicator Species Analysis (TWINSPAN), a polythetic divisive classification technique, and Detrended Correspondence Analysis (DECORANA), a divisive ordination method based on reciprocal averaging, were by far the best techniques available for analysing complex sample-by-species data arrays. The great value of these techniques is that a large array of species and samples, with large numbers of zero values, can be dealt with in an objective way independent of any prior knowledge about the samples other than the species present (Forster et al. 1990). Sites were initially grouped on the basis of their species lists using TWINSPAN and DECORANA. However, for the reasons summarised below and given in more detail in Equihua (1990), a fuzzy-clustering program was finally used instead of TWINSPAN to classify the sites. Species and sites were ordinated in two axes using DECORANA with all taxa being considered equally i.e. without downweighting, a procedure whereby the influence of rare taxa in the data on the ordination of the samples is minimised (Hill 1979b). Environmental variables were related to DECORANA ordination site scores using Spearman's rank correlation. Preliminary DECORANA analyses of both data matrices indicated that whilst there were two major axes of variation in both data sets, the variation appeared to be continuous i.e. discrete groups of quadrats with similar ground beetle associations or vegetation types were not clear. Data sets with continuous rather than disjunct variation are not suitable for classification using conventional classification algorithms such as TWINSPAN because they effectively force hard partitions on what is effectively non-discrete data (Equihua 1990). Where variation is continuous, classifications which allow objects to have memberships in more than one class are more appropriate. Classification algorithms of this type have been developed from fuzzy set theory. The fuzzy c-means algorithm used by Bezdek (1981) was implemented in Basic on an IBM compatible and was used to classify the 74 sites in both data sets. The first and second axes of the respective DECORANA ordinations were used as descriptor variables for each quadrat. The use of ordination axes as variables in the classification of data is considered to be better than using raw data since the ordination effectively summarises the major trends in the data set into a smaller number of dimensions that are easy to work with and minimises the potential error arising from the errors in species identification at individual sites (Equihua 1990). To avoid distortion of the analyses, six sites with less than 5 ground beetle species were not included in the initial DECORANA ordination of the Carabidae data set or in the fuzzy clustering of the DECORANA scores obtained (after Luff et al. 1989). The locations of these sites in the ordination space were calculated later from the DECORANA species scores, and these derived site scores inserted into the fuzzy classification providing membership values for the fuzzy groups already obtained.

Diversity indices

The ground beetle abundance data and vegetation percentage cover data were used to calculate William's index of diversity (alpha) values for each site (see Southwood 1978). These values were then used to calculate the mean indices of beetle and vegetation diversity for each of the end-groups recognised from the analyses of the beetle presence/absence data, and the mean index of vegetation diversity for each of the end-groups recognised from the analyses of the vegetation percentage cover data.

Comparison of ground beetle and vegetation analyses

Fuzzy clustering allocates sites to groups on the basis of membership values, but in order to compare site allocation between the groups obtained from analyses of the two data matrices it was necessary in each analysis to convert the fuzzy partition into a hard partition. This was easily achieved by assigning each site to the group for which it had the highest membership value, although it should be borne in mind that to construct a hard partition from a fuzzy one introduces precisely the same problems which fuzzy sets were developed to avoid (Equihua 1990). The comparison was based on a contingency table where the columns were the groups obtained from fuzzy clustering the ground beetle presence/absence data, the rows the groups from fuzzy clustering the vegetation percentage cover data. Groups were arranged in order to maximise entries along the main diagonal. The entries themselves were the counts of sites allocated to each combination of beetle and vegetation groups. If there was a perfect agreement between the two sets of groups, the off-diagonal elements will all be zero (Equihua 1990).

A log-likelihood ratio test (see Zar 1984) was conducted on the contingency table to test for associations between the two sets of groups. The G statistic in the log-likelihood ratio test was calculated using the following equation:

$$G = 4.605 \left[\sum \sum f_{ij} \log f_{ij} - \sum R_i \log R_i - \sum C_j \log C_j + n \log n \right]$$

where $\sum$ is the sum of the values; f_{ij} is the count in row i and column j of the table; R_i is the total of row i ; C_j is the total column j ; and n is the total number of sites in the table.

In addition, Procrustes rotation (Gower 1971; see Digby & Kempton 1987) was carried out using both sets of DECORANA site scores. This is a process whereby two configurations of points (ordinations) representing the same set of units (sites) are compared — one configuration is taken as fixed and the other is reflected, rotated and/or reduced to match it as closely as possible. Note that new scores are calculated for the rotated axes relative to the fixed axes scores. Simple correlations of site scores or ranks on each axis are not appropriate for use with several dimensions since it is the overall distance between points (sites) in multidimensional space that is important rather than their positions on individual axes. In the analysis presented here the scores derived from the ground beetle data were taken as fixed, and those obtained from the vegetation data rotated onto the beetle scores. Joining any two points on the resulting diagram corresponding to an individual site indicates how closely associated the two analyses were — the shorter the line the more similar the samples.

Results

Ground beetle data

Thirty-seven species of ground beetle were collected from the 74 sites on Ashtrees in 1990 (Table 1). Of these *Carabus prohemeticus*, *C. violaceus*, *Patrobis assimilis* and *Pterostichus diligens* were the most numerous and commonly captured. *Calathus melanocephalus* and *Nebria salina* were also numerous but only occurred at 41 and 32% of sites, respectively.

Ordination: Fig. 1 shows the axes 1 by 2 ordination plot, without downweighting of rare species, of the 74 sites in the data set. The eigenvalues for the ordination, which give some indication of the amount of community variation associated with each axis, were 0.314, 0.219, 0.146 and 0.119 for axes 1–4 respectively. These values suggested that axes 1 and 2 explained most of the between-site variation in the ground beetle communities and therefore axes 3 and 4 were not considered any further. The rank correlations between the environmental variables and site ordination scores are shown in Table 2, along with the correlations between the environmental variables and the number of ground beetle species per site. It can be seen that axis 1 was positively correlated with soil pH and negatively with soil percentage organic matter, and this is no doubt reflected in the fact that axis 1 was also negatively correlated with the percentage cover of woody plants i.e. heathers and related plants at each site. Axis 2 was positively correlated with the percentage cover of sedges at each site, and more so with the percentage cover of *Carex* and *Trichophorum*

Table 1. Number of ground beetles captured in pitfall traps at 74 sites on Ashtrees Heft during 1990, and the number of site occurrences

Species	Total number captured	Site occurrences
<i>Agonum fuliginosum</i> (Panzer)	15	12
<i>Amara aulica</i> (Panzer)	3	3
<i>A. communis</i> (Panzer)	5	4
<i>A. lunicollis</i> Schiodte	9	7
<i>Bembidion lampros</i> (Herbst)	4	2
<i>B. unicolor</i> (Chaudoir)	15	4
<i>Calathus melanocephalus</i> (Linnaeus)	119	30
<i>C. micropterus</i> (Duftschmid)	13	7
<i>Carabus arvensis</i> Herbst	29	24
<i>C. glabratus</i> Paykull	52	28
<i>C. nemoralis</i> Muller	22	14
<i>C. nitens</i> Linnaeus	4	3
<i>C. problematicus</i> Herbst	642	73
<i>C. violaceus</i> Linnaeus	134	53
<i>Cychrus caraboides</i> (Linnaeus)	1	1
<i>Dyschirius globosus</i> (Herbst)	1	1
<i>Leistus rufescens</i> (Fabricius)	7	7
<i>Loricera pilicornis</i> (Fabricius)	52	23
<i>Nebria brevicollis</i> (Fabricius)	25	11
<i>N. salina</i> Fairmaire	181	23
<i>Notiophilus aquaticus</i> (Linnaeus)	16	12
<i>N. biguttatus</i> (Fabricius)	1	1
<i>N. germinyi</i> Favel	1	1
<i>N. palustris</i> (Duftschmid)	18	15
<i>Olisthopus rotundatus</i> (Paykull)	1	1
<i>Patrobus assimilis</i> Chaudoir	281	70
<i>Pterostichus adstrictus</i> Eschscholtz	28	15
<i>P. aethiops</i> (Panzer)	55	30
<i>P. diligens</i> (Sturm)	113	52
<i>P. madidus</i> (Fabricius)	61	9
<i>P. melanarius</i> (Illiger)	7	5
<i>P. niger</i> (Schaller)	67	30
<i>P. nigrita</i> complex	59	27
<i>P. strenuus</i> (Panzer)	1	1
<i>P. versicolor</i> (Sturm)	3	2
<i>Synuchus nivalis</i> (Panzer)	3	3
<i>Trechus obtusus</i> Erichson	31	8

Total number of sites: 74, Total number of species: 37, Total number of individuals captured: 2079, Mean number of species per site $\pm$ SE: 8.27 ± 0.34 (min 3; max 17).

than with *Eriophorum* species. This suggests that some function of the openness of the vegetation was operating on the ground beetles and determining the location of the sites along axis 2. In addition, the number of ground beetle species per site was negatively correlated with soil percentage moisture, and therefore also with the percentage cover of mosses and sedges, and was positively correlated with soil dry bulk density along with total plant and grass-only species richness. Note that these figures only relate to the number of species per site and therefore do not indicate the effect of these environmental variables on particular species. Such detailed information was provided by the multivariate analyses, as is shown in the following section.

Table 2. Spearman rank correlation coefficients between ground beetle DECORANA site axes scores and environmental variables, between the number of ground beetle species per site and environmental variables, and between vegetation percentage cover DECORANA site axes scores and environmental variables (*P < 0.05; **P < 0.01; ***P < 0.001)

Environmental Variable	Ground beetle data			Vegetation data	
	Axis 1	Axis 2	Number of species per site	Axis 1	Axis 2
Soil pH	0.36**	n.s.	0.23*	0.44***	-0.26*
Soil % Moisture	n.s.	0.28*	-0.44***	-0.47***	0.49***
Soil Dry Bulk Density	n.s.	n.s.	0.38***	0.67***	-0.51***
Soil % Organic Matter	-0.32**	n.s.	n.s.	-0.38***	n.s.
% Cover All Grasses	n.s.	n.s.	n.s.	0.77***	-0.53***
% Cover All Woody Plants	-0.39***	n.s.	n.s.	-0.69***	n.s.
% Cover All Non-Woody Dicots	0.23	n.s.	0.41***	0.74***	n.s.
% Cover All Rushes	n.s.	n.s.	n.s.	0.58***	n.s.
% Cover All Sedges	n.s.	0.30**	-0.39**	-0.66***	0.69***
% Cover Sedges minus <i>Eriophorum</i>	n.s.	0.25*	n.s.	n.s.	0.53***
% Cover <i>Eriophorum</i> only	n.s.	n.s.	-0.27*	-0.67***	0.53***
% Cover All Mosses	n.s.	n.s.	-0.52***	-0.48***	n.s.
Total Plant spp. Richness	n.s.	-0.26*	0.36**	0.66***	n.s.
Grasses only spp. richness	n.s.	n.s.	0.41***	0.86***	-0.47***

Table 3. Centroids and mean beetle and plant alpha diversity indices ($\pm$ SE) for the 5 clusters derived from a fuzzy c-means clustering of the first two axes of the DECORANA ordination of the 1990 ground beetle presence absence data

Group Number	Centroids		Mean alpha diversity indices	
	Axis 1	Axis 2	Beetles	Plants
1	47.4	152.3	3.24 $\pm$ 0.38	3.06 $\pm$ 0.28
2	39.4	53.0	7.39 $\pm$ 1.30	2.67 $\pm$ 0.20
3	105.0	70.5	4.42 $\pm$ 0.38	2.87 $\pm$ 0.17
4	112.8	174.9	2.97 $\pm$ 0.33	2.10 $\pm$ 0.14
5	197.6	81.5	5.78 $\pm$ 0.87	3.49 $\pm$ 0.46

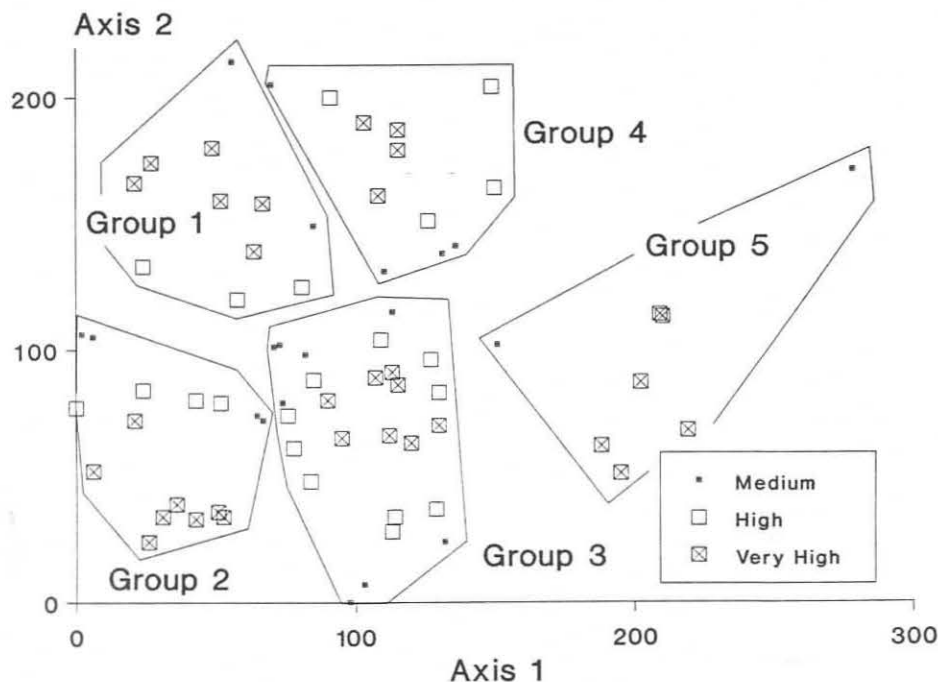


Fig. 1. Axis 1 by axis 2 plot of the DECORANA ordination of the ground beetle presence-absence data, without downweighting of rare species. Polygons enclose space containing the sites within each of the groups derived from a hard partition of a fuzzy c-means clustering of the ordination scores. An indication of membership value is shown for each site within each group (medium: 0.35–0.55; high: 0.56–0.75; very high: 0.76–1.00)

Classification by fuzzy clustering: The partition coefficient (a value between 0 and 1) provides a measure of the 'strength' of the clustering and reaches a maximum when the 'best' number of clusters is fitted. In the ground beetle analyses, the largest partition coefficient (0.463) was obtained for the classification of the DECORANA site scores based on 5 clusters. These groups are shown, after hard partitioning, in Fig. 1 and the centroids of each group are given in Table 3. The frequency of occurrence of ground beetle species within these groups is given in Table 4, and Table 5 gives the vegetation characteristics of the sites within these groups. The ground beetle groups were described as follows:

Group 1: contained roadside sites and some others which had suffered extensive disturbance e.g. high grazing pressure. These sites were particularly associated with *Carex nigra* and *Calluna vulgaris* vegetation. The ground beetle fauna of these sites consisted mainly of ubiquitous species such as *Patrobis assimilis* and *Carabus problematicus*, along with species with preference for damp areas (e.g. *Pterostichus diligens*) and highly invasive species (e.g. *Loricera pilicornis* and *Nebria salina*).

Group 2: sites in this group were associated with *Calluna*-dominated heath, and contained ground beetles associated with shady ground (e.g. *Calathus micropterus*, *Carabus violaceus* and *Pterostichus diligens*) as well as species associated with dry, open ground (e.g. *Carabus arvensis* and *Calathus melanocephalus*).

Group 3: contained sites from *Calluna*/*Molinia caerulea* dominated grassland which appeared to be verging on bog. The ground beetle species included those associated with damp places (e.g. *Carabus violaceus*) with well developed vegetation (e.g. *Pterostichus niger*).

Table 4. The frequency of occurrence of ground beetle species within the groups derived from fuzzy clustering of the first two axes of the DECORANA ordination of the 1990 ground beetle presence/absence data, where a species occurs in >20% of the sites in one of the groups (D = 21–40%; C = 41–60%; B = 61–80%; A = 81–100%). The species order is derived from the ordination of the species along DECORANA axis 1

Species	Ground beetle fuzzy groups					
	n =	1 11	2 16	3 26	4 13	5 8
<i>Calathus micropterus</i>	—	—	C	—	—	—
<i>Notiophilus aquaticus</i>	—	—	C	—	—	—
<i>Pterostichus adstrictus</i>	C	—	C	—	—	—
<i>Carabus arvensis</i>	—	—	B	D	—	—
<i>Leistus rufescens</i>	—	—	D	—	—	—
<i>Pterostichus diligens</i>	A	A	A	C	A	—
<i>Loricera pilicornis</i>	C	—	D	D	D	D
<i>Pterostichus aethiops</i>	D	—	B	D	—	D
<i>Carabus nemoralis</i>	D	—	D	—	—	—
<i>Patrobus assimilis</i>	A	A	A	A	A	B
<i>Calathus melanocephalus</i>	—	—	B	C	—	D
<i>Nebria salina</i>	B	—	—	—	A	—
<i>Carabus problematicus</i>	A	A	A	A	A	A
<i>C. glabratus</i>	—	—	C	C	—	C
<i>C. violaceus</i>	C	—	A	A	D	B
<i>Notiophilus palustris</i>	—	—	D	D	—	D
<i>Pterostichus niger</i>	—	—	C	C	D	C
<i>Agonum fuliginosum</i>	—	—	—	D	D	D
<i>Pterostichus nigrita</i>	—	—	—	D	B	B
<i>Nebria brevicollis</i>	D	—	—	—	D	C
<i>Synuchus nivalis</i>	—	—	—	—	—	D
<i>Pterostichus madidus</i>	—	—	—	—	—	B
<i>Trechus obtusus</i>	—	—	—	—	—	A
<i>Amara aulica</i>	—	—	—	—	—	D
<i>Bembidion unicolor</i>	—	—	—	—	—	C
<i>Pterostichus melanarius</i>	—	—	—	—	—	B

Group 4: sites in this group were particularly associated with bog vegetation such as *Eriophorum* spp. and *Polytricum commune*, with the ground beetle fauna containing those species especially preferring damp and wet conditions (e.g. *Pterostichus nigrita* and *P. diligens*).

Group 5: the majority of sites in this group were on mineral soil and contained a wide range of grass species (e.g. *Nardus stricta*, *Anthoxanthum odoratum*, *Holcus lanatus* etc.). Similarly a wide range of ground beetle species were associated with this group, particularly *Trechus obtusus*, *Pterostichus madidus* and *P. melanarius*. Mean beetle and plant alpha diversity indices for these 5 groups are shown in Table 3. It can be seen that the *Calluna*-dominated heath sites (group 2) and those grassland sites over mineral soil (group 5) had the highest ground beetle alpha diversities, while the bog (group 4) and roadside (group 1) sites had the lowest. The mineral soil grassland and bog sites also had the highest and lowest plant alpha diversities, respectively. However, there was no obvious direct relationship between beetle and plant alpha indices, since the roadside sites also had a relatively high plant alpha diversity.

From Table 5 it can be seen that the heather/grassland dominated sites (groups 1–4) were very similar to each other in plant species composition, but all were markedly different

Table 5. Vegetation characteristics of the sites within each of the groups derived from fuzzy clustering of the first two axes of the DECORANA ordination of the 1990 ground beetle presence/absence data. The frequency of occurrence of each plant species within the groups, where a species occurs in >20% of the sites in one of the groups, is shown (D = 21–40%; C = 41–60%; B = 61–80%; A = 81–100%). The figures in parenthesis give the mean percentage cover $\pm$ SE of that species within the sites of group

Species	Ground beetle fuzzy groups					
	n=	1 11	2 16	3 26	4 13	5 8
<i>Eriophorum vaginatum</i>	—		D (4.3 ± 3.1)	C (7.0 ± 2.1)	C (11.5 ± 4.7)	—
<i>Sphagnum palustre</i>	—		—	D (1.2 ± 0.6)	—	—
<i>Eriophorum angustifolium</i>	—		D (2.9 ± 2.0)	C (2.8 ± 0.9)	C (7.4 ± 3.3)	—
<i>Sphagnum recurvum</i>	—		—	D (0.4 ± 0.2)	C (1.3 ± 0.5)	—
<i>Calluna vulgaris</i>	B (10.4 ± 4.5)		A (24.4 ± 6.0)	B (16.2 ± 4.1)	D (5.6 ± 3.2)	—
<i>Vaccinium myrtillus</i>	D (1.3 ± 0.6)		—	D (1.6 ± 0.6)	—	—
<i>Polytricum commune</i>	C (3.8 ± 1.6)		B (2.2 ± 0.8)	C (3.4 ± 1.0)	B (6.7 ± 3.6)	D (1.7 ± 1.3)
<i>Deschampsia flexuosa</i>	A (4.9 ± 1.6)		A (7.2 ± 1.6)	A (5.7 ± 1.1)	B (7.6 ± 2.2)	D (0.6 ± 0.4)
<i>Pleurozium schreiberi</i>	D (0.3 ± 0.2)		D (0.6 ± 0.3)	C (0.9 ± 0.3)	D (0.5 ± 0.3)	—
<i>Molinia caerulea</i>	B (7.8 ± 3.1)		A (11.0 ± 3.2)	B (15.9 ± 3.5)	B (11.1 ± 5.1)	C (5.1 ± 2.6)
<i>Trichoporum cespitosum</i>	D (1.0 ± 0.6)		—	D (2.6 ± 1.3)	—	—
<i>Carex nigra</i>	A (18.4 ± 4.3)		A (15.5 ± 3.6)	A (12.4 ± 2.3)	B (22.0 ± 5.1)	A (9.1 ± 3.3)
<i>Juncus squarrosus</i>	B (7.6 ± 3.0)		D (1.7 ± 0.9)	D (1.3 ± 0.8)	D (3.1 ± 0.2)	—
<i>Festuca ovina</i>	B (6.2 ± 2.1)		B (6.0 ± 1.4)	B (4.7 ± 1.2)	D (6.0 ± 2.5)	C (1.9 ± 1.3)
<i>Potentilla erecta</i>	—		D (1.3 ± 0.5)	D (1.2 ± 0.5)	—	B (1.8 ± 0.7)
<i>Luzula multiflora</i>	—		D (0.2 ± 0.1)	D (0.4 ± 0.1)	—	D (0.4 ± 0.2)
<i>Galium saxatile</i>	D (2.0 ± 1.8)		C (1.9 ± 0.8)	D (1.7 ± 1.0)	D (0.5 ± 0.3)	D (2.0 ± 1.9)
<i>Nardus stricta</i>	D (5.5 ± 3.4)		D (10.8 ± 3.4)	D (7.8 ± 3.0)	D (5.2 ± 3.4)	B (23.6 ± 7.6)
<i>Rhytidiadelphus squarrosus</i>	D (0.3 ± 0.2)		D (0.7 ± 0.3)	—	—	—
<i>Anthoxanthum odoratum</i>	C (1.6 ± 0.9)		C (2.9 ± 1.0)	D (1.1 ± 0.4)	D (0.2 ± 0.1)	B (5.9 ± 2.2)
<i>Juncus effusus</i>	—		—	—	—	B (11.7 ± 5.1)
<i>Deschampsia caespitosa</i>	—		—	—	—	B (0.4 ± 0.3)
<i>Carex panicea</i>	—		—	—	—	D (1.3 ± 0.9)
<i>Holcus lanatus</i>	—		—	—	—	B (4.2 ± 1.1)
<i>Cirsium palustre</i>	—		—	—	—	D (0.6 ± 0.4)
<i>Festuca rubra</i>	—		—	—	—	D (0.5 ± 0.4)
<i>Trifolium repens</i>	—		—	—	—	D (1.4 ± 0.8)
<i>Agrostis capillaris</i>	D (2.7 ± 1.8)		—	D (1.7 ± 0.8)	D (3.0 ± 2.7)	B (4.7 ± 1.5)
<i>A. stolonifera</i>	—		—	—	—	D (1.0 ± 0.6)
<i>Cynosurus cristatus</i>	—		—	—	—	C (1.1 ± 0.7)
<i>Juncus articulatus</i>	—		—	—	—	D (10.1 ± 8.0)

from the mineral soil grassland sites (group 5). The *Calluna* dominated heath and *Calluna*/*Molinia*-dominated grassland sites (groups 2 & 3) were most similar in ground beetle species composition, while the mineral soil grassland sites (group 5) were quite different from all the other groups except the *Calluna*/*Molinia*-dominated grassland (group 3). It is therefore clear from Tables 3–5 that although there was considerable overlap in species composition between some of the groups, each group contained a unique association of ground beetles and plants.

Vegetation data

Ordination: Fig. 2 shows the axes 1 by 2 ordination plot, without downweighting of rare species, of the 74 sites in the data set. The eigenvalues for the ordination were 0.749, 0.495, 0.234 and 0.174 for axes 1–4 respectively. These values suggested that axes 1 and 2 explained most of the between-site variation in the vegetation communities and therefore axes 3 and 4 were not considered any further. The rank correlations between the environmental variables and site ordination scores are shown in Table 2. Axis 1 was highly significantly related to all 4 soil variables measured (dry bulk density, percentage water, pH and percentage organic matter) and this is reflected in the correlations with vegetation types across the axis. Axis 2 was mainly correlated with soil bulk density and percentage soil water, which is emphasised by the fact that it was positively correlated with the percentage cover of sedges and negatively with the percentage cover of grasses.

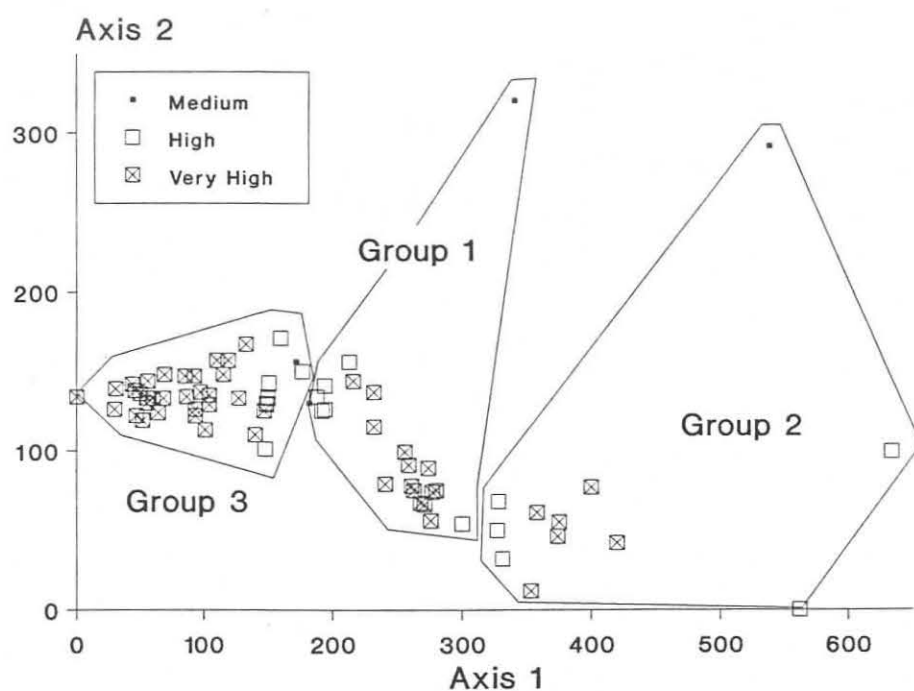


Fig. 2. Axis 1 by axis 2 plot of the DECORANA ordination of the vegetation percentage cover data, without downweighting of rare species. Polygons enclose space containing the sites within each of the groups derived from a hard partition of a fuzzy c-means clustering of the ordination scores. An indication of membership value is shown for each site within each group (medium: 0.35–0.55; high: 0.56–0.75; very high: 0.76–1.00)

Table 6. Centroids and mean plant alpha diversity indices ($\pm$ SE) for the 3 clusters derived from a fuzzy c-means clustering of the first two axes of the DECORANA ordination of the 1990 vegetation percentage cover data

Group Number	Centroids		Mean plant alpha
Group Number	Axis 1	Axis 2	diversity indices
1	251.2	99.8	2.94 ± 0.16
2	401.3	63.3	3.36 ± 0.33
3	92.8	135.8	2.53 ± 0.26

Classification by fuzzy clustering: The largest partition coefficient (0.668) was obtained for the classification of the DECORANA site scores based on 4 clusters. However, the ecological interpretation of the clusters, based on the plant species present, was much clearer for the classification of the site scores based on 3 groups. The partition coefficient for this classification was 0.643. These 3 groups are shown, after hard partitioning, in Fig. 2 and the centroids of each group are given in Table 6. The frequency of occurrence of plant species, and hence vegetation characteristics, within these groups is given in Table 7. The vegetation groups were described as follows:

Group 1: sites in this group contained a typical moorland grass community being particularly dominated by *Molinia caerulea*, *Nardus stricta* and *Festuca ovina* and the sedge *Carex nigra*.

Group 2: contained sites on mineral soil with a wide range of grass species e.g. *Nardus stricta*, *Agrostis capillaris*, *Anthoxanthum odoratum* and *Holcus lanatus*. In addition, rushes (*Juncus effusus* and *J. articulatus*) featured prominently in the sites.

Group 3: contained sites with a range of heather/bog species, especially *Calluna vulgaris*, *Carex nigra*, *Eriophorum* spp., *Polytricum commune* and *Molinia caerulea*. Mean plant alpha diversity indices for these three groups are given in Table 6. The mineral soil grassland sites (group 2) had the highest and the heather/bog sites (group 3) the lowest alpha diversities, but the indices for all three groups were very close. From Table 7 it can be seen that all three groups were very similar in plant species composition, with the moorland grassland sites (group 1) and the mineral soil grassland sites (group 2) being most similar.

Analysis of the vegetation data set therefore grouped the sites into 3 broad vegetation categories — two grassland and one heather/bog.

Comparison of ground beetle and vegetation analyses

Contingency table: Table 8 shows the contingency table giving the number of sites allocated to each combination of ground beetle and vegetation fuzzy clustered groups. Although the calculated G statistic suggests that there was a significant association between certain ground beetle groups and vegetation groups within the table, it can be seen from Table 8 that the closeness of this association varied between groups. Beetle group 5 and vegetation group 2 were closely associated, with the majority (75%) of the sites in beetle group 5 occurring in vegetation group 2. By contrast, beetle groups 1–4 were less closely associated with vegetation groups 1 and 3, with between 54 and 63% of the sites in beetle groups 1–4 occurring in vegetation group 3 and between 30 and 37% of the sites occurring in vegetation group 1.

Table 7. The frequency of occurrence of plant species within each of the groups derived from fuzzy clustering of the first two axes of the DECORANA ordination of the 1990 vegetation percentage cover data, where a species occurs in >20% of the sites in one of the groups (D = 21–40%; B = 61–80%; A = 81–100%). The figures in parenthesis give the mean percentage cover $\pm$ SE of that species within the sites of the group

Species	Ground beetle fuzzy groups		
	1 n= 22	2 12	3 40
<i>Eriophorum vaginatum</i>	—	—	C (11.3 $\pm$ 2.3)
<i>Eriophorum angustifolium</i>	—	—	B (7.3 $\pm$ 1.5)
<i>Sphagnum recurvum</i>	—	—	D (1.0 $\pm$ 0.3)
<i>Calluna vulgaris</i>	D (1.6 $\pm$ 0.6)	—	A (24.4 $\pm$ 3.4)
<i>Vaccinium myrtillus</i>	—	—	D (1.5 $\pm$ 0.4)
<i>Polytricum commune</i>	C (1.8 $\pm$ 0.9)	—	B (5.6 $\pm$ 1.3)
<i>Deschampsia flexuosa</i>	A (4.9 $\pm$ 1.0)	D (0.8 $\pm$ 0.4)	A (7.9 $\pm$ 1.1)
<i>Pleurozium schreiberi</i>	—	D (0.4 $\pm$ 0.3)	C (0.9 $\pm$ 0.2)
<i>Molinia caerulea</i>	A (20.6 $\pm$ 4.3)	D (1.6 $\pm$ 1.0)	B (10.8 $\pm$ 1.9)
<i>Carex nigra</i>	A (18.4 $\pm$ 3.1)	C (3.2 $\pm$ 1.4)	A (17.4 $\pm$ 2.2)
<i>Juncus squarrosus</i>	C (5.1 $\pm$ 1.9)	—	D (1.8 $\pm$ 0.8)
<i>Festuca ovina</i>	A (11.7 $\pm$ 1.4)	B (4.1 $\pm$ 1.6)	D (1.8 $\pm$ 0.5)
<i>Potentilla erecta</i>	C (1.2 $\pm$ 0.4)	C (1.7 $\pm$ 0.6)	—
<i>Luzula multiflora</i>	C (0.8 $\pm$ 0.4)	C (0.6 $\pm$ 0.2)	—
<i>Galium saxatile</i>	C (3.0 $\pm$ 1.4)	C (2.9 $\pm$ 1.3)	—
<i>Nardus stricta</i>	B (17.4 $\pm$ 4.0)	B (26.7 $\pm$ 6.8)	—
<i>Rhytidadelphus squarrosus</i>	—	D (0.6 $\pm$ 0.3)	—
<i>Anthoxanthum odoratum</i>	A (2.0 $\pm$ 0.5)	A (6.7 $\pm$ 1.6)	—
<i>Juncus effusus</i>	C (2.8 $\pm$ 1.3)	C (10.4 $\pm$ 4.1)	—
<i>Deschampsia caespitosa</i>	—	D (1.6 $\pm$ 0.9)	—
<i>Carex panicea</i>	—	D (1.1 $\pm$ 0.6)	—
<i>Holcus lanatus</i>	—	C (3.3 $\pm$ 1.1)	—
<i>Festuca rubra</i>	—	D (0.4 $\pm$ 0.4)	—
<i>Trifolium repens</i>	—	D (1.0 $\pm$ 0.5)	—
<i>Agrostis capillaris</i>	C (1.6 $\pm$ 0.6)	B (10.8 $\pm$ 3.0)	—
<i>A. stolonifera</i>	—	D (1.1 $\pm$ 0.5)	—
<i>Cynosurus cristatus</i>	—	D (1.4 $\pm$ 0.8)	—
<i>Juncus articulatus</i>	—	D (6.9 $\pm$ 5.4)	—
<i>Poa pratensis</i>	—	D (4.2 $\pm$ 3.1)	—

Table 8. Contingency table showing the number of sites allocated to each combination of groups obtained from fuzzy c-means clustering of the first two axes of the DECORANA ordinations of 1990 ground beetle presence/absence and vegetation percentage cover data sets. The G statistic for the log-likelihood ratio test was calculated using the equation in the text

		Ground beetle fuzzy groups					Row Totals
		5	3	2	4	1	
Vegetation	2	6	3	1	1	1	12
fuzzy	3	1	15	10	8	6	40
groups	1	1	8	5	4	4	22
Column Totals		8	26	16	13	11	

G statistic = 17.08, 8 d.f., $P < 0.05$

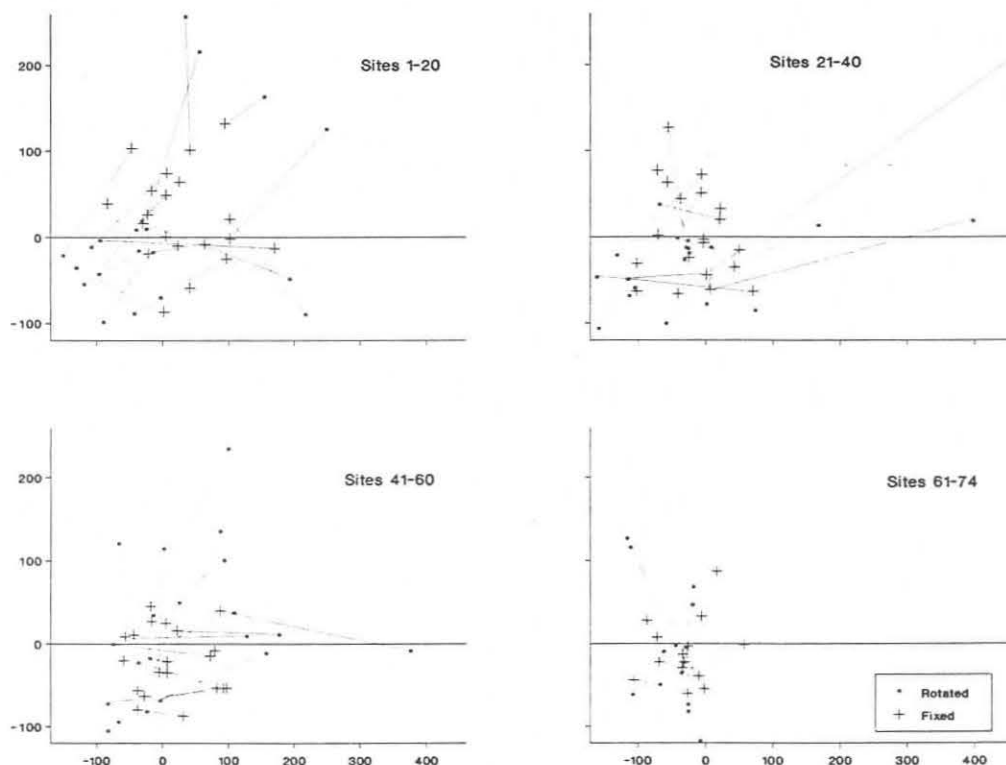


Fig. 3. Axis 1 by axis 2 configuration of the 74 sites after Procrustes rotation of the vegetation DECORANA ordination scores onto the ground beetle DECORANA ordination scores. Lines connect sites from the rotated ordination to their respective fixed points in the beetle ordination

Procrustes rotation: Fig. 3 shows the configuration of the 74 sites after Procrustes rotation of the vegetation ordination scores to fit the ground beetle ordination scores. The lines connect sites from the rotated ordination to their respective fixed points in the beetle ordination, and it can be seen that the largest residuals were associated with 3 sites (35, 37 and 43). These sites were surrounded by a number of different vegetation types and it would therefore appear that an 'edge-effect' was operating whereupon ground beetle species from these other habitats were captured at these sites — Baars (1979) found that some large and medium-sized ground beetle species had areas of activity of up to 50–100 ha and could move 10 m in a day. In addition to these extremely high values, it can be seen that the majority of the distances between fixed and rotated points were quite large. Indeed, the mean distance ($\pm$ SE) between all 74 fixed and rotated points was 128 ± 10.2 axis units, with 85% of rotated points being more than 50 axis units from their respective fixed point. This suggests that the general fit of the vegetation ordination to the beetle ordination was not very good and thereby justifies the statement made previously that there was variations in the closeness of the associations between the vegetation and beetle groups recognised.

Discussion

The most important advantage of pitfall traps is that they collect large samples of invertebrates throughout the time that they are in place (Coulson & Butterfield 1985). Pitfall trapping has been criticised as a sampling method, since the number of individuals

caught depends on the activity of the species as well as their abundances (Southwood 1978), but it has been shown that classifying sites by their pitfall catches is reasonable so long as the analysis is based on catch and not absolute densities (Luff & Eyre 1988).

Also vegetation and invertebrate communities differ markedly with regard to ease of sampling. The vegetation at a site is relatively easy to sample (being stable in occurrence and normally present in a recognisable form throughout most of the year), whereas it is much more difficult to sample invertebrates accurately (as they are mobile with recognisable forms present for only part of the year). It is therefore important that the results obtained from multivariate analysis of invertebrate data are considered carefully, before any firm conclusions are drawn (McCracken 1990).

Five ground beetle communities were recognised from the analyses, each group having a close association with a particular vegetation type, whereas only three broad vegetation types were recognised from similar analyses of the vegetation data set. In other words, a better indication of the variation in habitat present over the range of sample sites was provided by using the beetle data in association with the vegetation data, rather than by using the vegetation data alone.

It would appear that the structure of the vegetation, rather than the basic species composition at each sample site influenced the range of beetles present, since although four of the beetle groups were very similar in plant species composition, the percentage cover of species within each group was markedly different. In addition, the most diverse ground beetle fauna was found on the *Calluna*-dominated heath sites possessing relatively low plant diversities. A possible explanation for this is that at the latter sites the *Calluna*-dominated heath did not form a continuous expanse but instead consisted of a fragmented patchwork within other vegetation types. Therefore although plant diversity was low at these sites, the fragmentation of the heath and the diversity of surrounding vegetation types resulted in a greater of ground beetle species being present on these sites.

Ordination of the ground beetle presence/absence data indicated that the distribution of the carabid communities at these sites was primarily related to substratum variables, especially soil pH and percentage organic matter. Distribution of the vegetation communities recognised from ordination of the vegetation percentage cover data was also highly correlated with the range of soil environmental variables measured. This study therefore complements other studies in uplands and in managed grasslands which have suggested that invertebrate (Coulson & Butterfield 1985; McCracken & Foster 1993), especially Carabidae (Luff et al. 1989; Eyre et al. 1990), and vegetation (Smith 1988; Smith & Charman 1988; Coulson et al. 1990; Equihua 1990) community structure is usually related to soil structure and moisture.

In addition, the distribution of the ground beetle communities at the sites studied was also related to some function of the openness of the vegetation. Again this compares well with the results of previous studies e.g. vegetation development was identified by Gardner (1991) as an important factor determining the composition of the carabid community of *Calluna*-dominated heath, and the amount of tussock vegetation present was found by Rushton et al. (1990) to influence the ground beetle communities on an area of limestone grassland.

The results presented above have shown that the presence of *Calluna*-dominated heath at the sample sites was important in maintaining a diverse ground beetle fauna. As already stated, increased awareness of the impact of intensive sheep rearing on semi-natural vegetation has led to concern that these habitats are under threat. *Calluna vulgaris* is considered to be particularly at risk because of its susceptibility to overgrazing. Indeed, between 1976 and 1989 the area where *C. vulgaris* was present at greater than 50% cover on Ashtree Heft (the area under study here) declined by 40%, and this decrease in heather cover corresponded with an increase in the sheep stocking rate over that period (Rushton & Byrne 1990).

Therefore, if livestock numbers in hill areas at present levels and the general regression in such plant communities continues, then the above findings suggest that detrimental effects on the ground beetle communities in these areas could also be expected.

In the present study, comparison of the groups derived from the analyses of the beetle and plant data sets indicated that there were variations in the closeness of the associations between the ground beetle and plant communities recognised.

Although each group recognised contained a unique association of ground beetles and plants, there was considerable overlap in species composition between some of the groups. Gardner (1991) also showed a good correlation between the classifications of ground beetles and plants from the same series of sites, but found that knowledge of one set of data could not be used to predict the other. However, both the latter and the present findings were perhaps not surprising since they were based solely on the results obtained from data collected in one sampling season. Many biological processes are considered to be Markovian, in the sense that the changes in any one time period are likely to be dependent on the point from which they start (Usher 1979). Therefore although the beetle community at a particular site may show a good correlation with the vegetation present at that site, one would expect the exact composition of beetle species to be dependent on what that particular plant community had developed from, i.e. on the stability of the system, and on the diversity of surrounding vegetation types. Knowledge gained over a number of years of any changes on a particular site is required before accurate predictions of future changes can be made.

Much remains to be discovered about ground beetle and other invertebrate populations in these hill areas, and in view of the speed with which plant communities with high conservation value are disappearing from these areas, it is suggested that such research needs to be carried out urgently. The Ashtrees project is still in its early stages and more data are required before the accuracy of any associations can be tested. However, the results presented here suggest that once enough baseline information is available (e.g. collected over a number of years), the analyses used should allow predictions of invertebrate changes for any associated changes in vegetation cover to be made. The long-term nature of the project will allow valuable information on the effect of reduced stocking rates and/or strategic grazing regimes on heather regeneration and animal outputs to be monitored. The information so obtained will be of use for developing methods of maintaining productivity and effective utilisation of grass and natural vegetation in the hills and uplands, while ensuring that farming is viable and environmentally sympathetic.

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